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ANTS OF THE DOMINICAN AMBER (HYMENOPTERA: FORMICIDAE). 3. THE SUBFAMILY DOLICHODERINAE

By Edward O. Wilson
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

The Dolichoderinae, in particular the species of *Azteca* and *Iridomyrmex*, are by a wide margin the most abundantly represented ants in the Dominican amber. They are also exceptional in the number of genera occurring in the amber but not in the modern fauna of the Greater Antilles. In other words the Dolichoderinae appear to have undergone a considerable amount of retreat entailing local extinction since early Miocene times, and for this reason alone the fossil species deserve close attention. In the present review I have relied principally on the large collections I have assembled for the Museum of Comparative Zoology during the past 10 years, supplemented substantially by material loaned by Dr. Robert E. Woodruff. All of the holotypes (except *Dolichoderus dibolia*) and most of the paratypes have been deposited in the Museum of Comparative Zoology. The holotype of *D. dibolia* and a few paratypes have been placed in the Florida State Collection of Arthropods, Gainesville, Florida. Earlier parts of this series have dealt with extinct myrmicine genera and the ecitonine army ants respectively (Wilson, 1985a, b).

Dolichoderus

This genus of large, slender ants is composed today of 8 species limited to the moist tropical forests of South America. The colonies are mostly or exclusively arboreal. The species to be described below is clearly a member of the distinctive *attelaboides* group, which ranges from the Amazonian region of Bolivia north to Trinidad.

Dolichoderus dibolia, new species
(Fig. 1)

Diagnosis (worker). Similar to the living species *D. attelaboides* and *D. imbecillus,* particularly in its attenuated occipital "neck" and overall body shape (including especially the alitrunk and propodeal spines) but differs from both forms in its somewhat larger size; proportionately thicker mesothorax; lower, more rounded petiolar node (quadrate in side view in the case of *attelaboides* and *imbecillus*), and much longer anterior petiolar peduncle.

The name *dibolia,* Greek for lance, refers to the strongly developed propodeal spines.

Holotype worker. Length of alitrunk 3.7 mm. With moderately abundant, coarse, erect hairs, especially on the antennal scape. Sculpturing not determinable due to the obscuring of much of the body surface.

Monacis

The genus *Monacis* may eventually be fused with other blocks of the Dolichoderini (see Brown, 1973, who synonymizes it under *Dolichoderus*), but until a thoroughgoing revision of the tribe is completed I regard it as both prudent and convenient to treat this genus as a separate entity. For the moment all the New World species placed in *Monacis* (Kempf, 1959) are distinguished by their possession of angulate or spiny pronotal humeri and laterally mar-

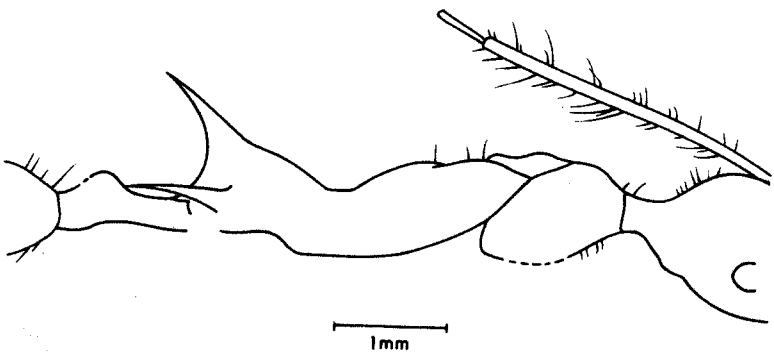

Fig. 1. *Dolichoderus dibolia* worker holotype, side view of body.

ginate mesonotum. Moreover, all recognized *Monacis* are Neotropical. Living members of the genus are almost wholly limited to the mainland from southern South America to southern Mexico, and all evidently nest arboreally. *M. bispinosa,* the most widespread species, also occurs on Trinidad and has been recorded, quite anomalously, from St. Thomas in the Virgin Islands (Mayr, 1862). The latter record was based on a single queen and is almost certainly an error—or at most represents a population introduced by human commerce. No other *Monacis* has been found in the remainder of the West Indies north of Trinidad, despite the fact that the workers of most of the species, including *M. bispinosa,* are large, conspicuous insects.

The two species described below from the Dominican amber are typical *Monacis* not much different from two species (*rufescens* and *laminatus* respectively) in the living fauna. They are of exceptional significance because of the current absence of the genus from the Greater Antilles.

Monacis caribbaea, new species
(Fig. 2)

Diagnosis (worker). A relatively small (Pronotal Width including humeral spines 0.49–0.66 mm), slender species resembling the modern *M. rufescens* of the Brazilian Amazon, differing from *rufescens* in its very sparse body pilosity and the more sharply angulate "shelf" separating the dorsal and declivitous (posterior) faces of the propodeum. *M. caribbaea* is also light reddish brown as opposed to light reddish yellow in *rufescens,* although its color might well have been altered during fossilization.

Holotype worker. Head Width 0.80 mm, Pronotal Width 0.51 mm. Alitrunk and petiole densely, finely, and evenly punctate, opaque; head still more finely punctate, grading to shagreened, and feebly shining. Body almost devoid of standing pilosity. Body mostly dark reddish brown, legs and parts of petiole and gaster light reddish brown.

Paratype workers. Eleven specimens in as many amber pieces: 2 from Palo Quemado (Pronotal Width of first 0.47 mm, second not measured), one from Bayaguana (no measurement), and 8 with no further locality within the Dominican Republic (Pronotal Width 0.49–0.66 mm).

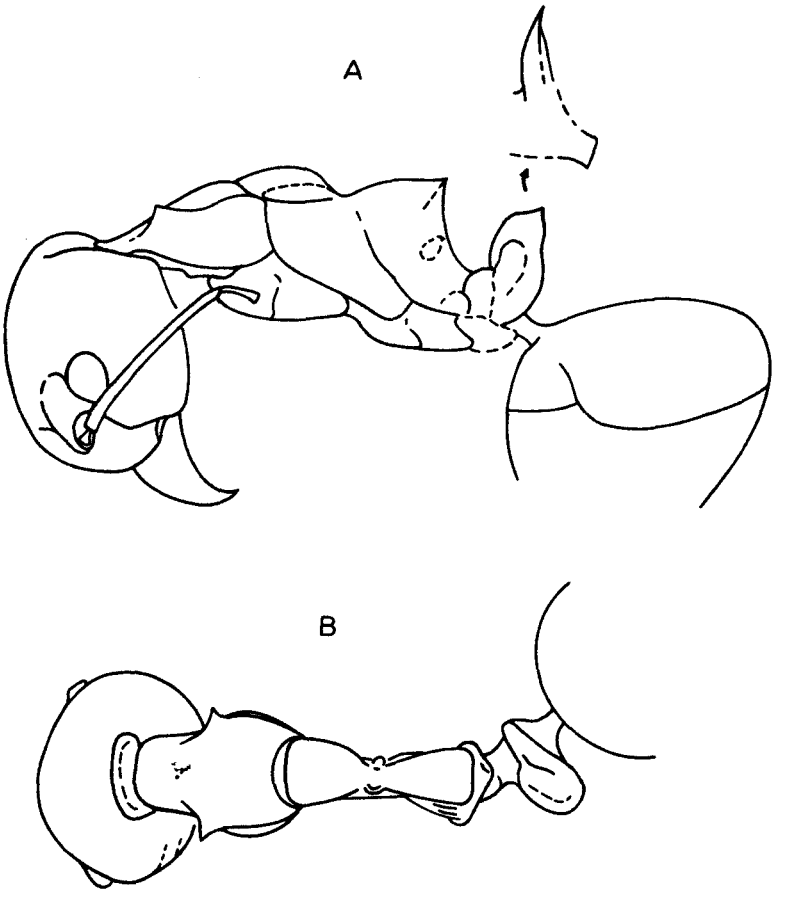

Fig. 2. *Monacis caribbaea* worker holotype: A, side view; B, dorsal view.

The pronotal humeri of the *caribbaea* types vary considerably, from well defined spines as in the holotype to simple acute angles approaching the condition that characterizes the second fossil species, *prolaminata*.

Monacis prolaminata, new species
(Fig. 3)

Diagnosis (*worker*). A relatively large, robust species closely resembling the living *M. laminata* of northern South America and

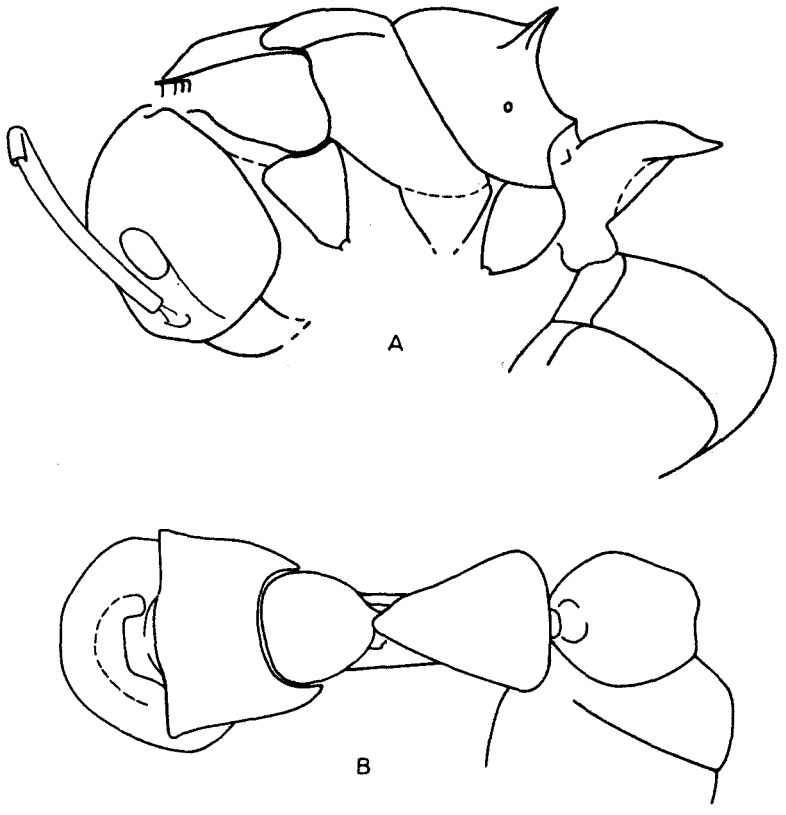

Fig. 3. *Monacis prolaminata* worker holotype: A, side view; B, dorsal view.

Central America, differing in the concave dorsal border of the petiolar scale viewed in full face (as opposed to strongly convex in *laminata*).

Holotype worker. Head Width 1.07 mm, Pronotal Width 0.93 mm. Dorsum of alitrunk shallowly rugoreticulate, the rugae longitudinally oriented on the mesonotum; spaces within the rugoreticular cells densely punctate; the whole surface entirely opaque but with reflections from the numerous evenly packed punctures giving the alitrunk a silvery, "sparkling" appearance. Head, petiole, and abdomen variably punctulate to shagreened and feebly shining. Body almost wholly devoid of standing pilosity. Body uniformly

blackish brown, appendages light to medium brown. Dominican Republic amber: no further locality.

Paratype workers. Five specimens in 4 amber pieces: one from Palo Quemado (Pronotal Width 1.11 mm), 4 others from Dominican amber with no further locality, 2 of which are in one piece (Pronotal Width 0.90–1.30 mm).

Hypoclinea

The modern genus *Hypoclinea* as presently defined is nearly cosmopolitan (absent in Africa) and highly diverse in anatomy and behavior. At least 15 species compose the living Neotropical fauna, almost all confined to the mainland of Mexico, Central America, and South America. The most widespread form, *H. lutosa,* occurs from Brazil to Trinidad and southern Mexico. It has also been recorded from St. Vincent in the southern part of the Lesser Antilles, where it is quite rare (Forel, 1893). *Hypoclinea* is apparently absent in the remainder of the West Indies, including all of the Greater Antilles, a circumstance giving the Dominican amber species to be described below more than ordinary biogeographic importance.

Hypoclinea primitiva, new species
(Fig. 4)

Diagnosis (worker). A medium-sized (Head Width 0.6–0.7 mm), slender species with several primitive traits for *Hypoclinea* overall, including a relatively unmodified alitrunk, smoothly rounded propodeum, simple petiolar scale, and a "generalized" head shape with reference to the Dolichoderini in general. Closest in appearance to *H. germaini* of South America among living species; *germaini* differs from *primitiva,* however, in having a blunt, transverse ridge that separates the dorsal and declivitous faces of the propodeum, as well as more flattened pro- and mesonota (both of these traits are reasonably interpreted as having been derived in evolution).

The name *primitiva* alludes both to the antiquity of the species and to the set of traits just cited that are provisionally interpreted to be primitive within the genus and perhaps even in the Dolichoderinae as a whole.

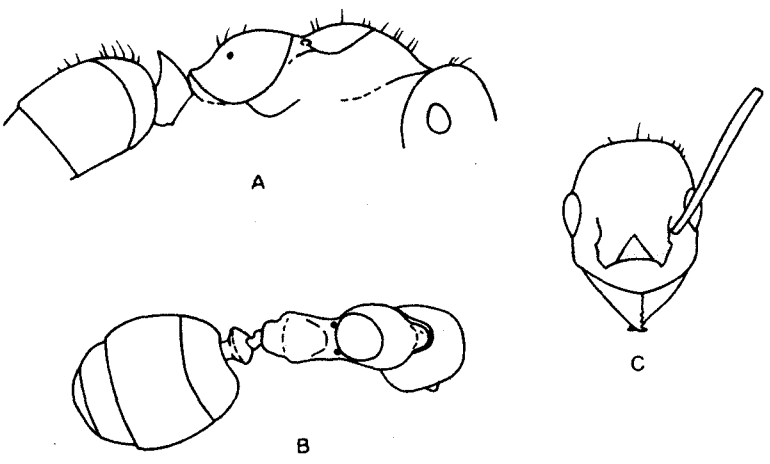

Fig. 4. *Hypoclinea primitiva* worker holotype: A, side view of body; B, dorsal view of body; C, head.

Holotype worker. Head Width 0.68 mm, Head Length 0.93 mm, Pronotal Width 0.56 mm, Scape Length 0.87 mm, Eye Length 0.26 mm. Posterior half of head bearing scattered foveae with the interspaces weakly shagreened and feebly shining. Rest of the body uniformly and lightly shagreened and feebly shining. Body uniformly light reddish brown. Dominican Republic amber: no further locality.

Paratype workers. Four workers: 2 in one amber piece from La Toca, associated with *Azteca alpha* workers (Head Width of one 0.64 mm, other not measured); two others in separate pieces originating from unknown localities (one with Head Width 0.66 mm, other not measured).

Azteca and *Iridomyrmex*

The large and complex genera *Azteca* and *Iridomyrmex* have proved difficult to separate in their entirety by means of external anatomy (a striking difference in the proventriculus makes the cleavage easier when this internal organ can be examined). The classification of fossil material is therefore difficult, since only external structures are usually preserved.

The problem is further complicated by the separation of workers, queens, and males into different amber pieces, so that most linkages across castes and sexes can only be guessed. In the case of the Dominican amber, however, I was able to solve the problem in part by the discovery of three miniature "Rosetta stones": 3 amber pieces with closely intermingled workers and males of the commonest species of *Azteca* (*A. alpha*). One of the pieces also contains a male pupa, further supporting the interpretation that the associated workers and males belonged to the same colony and were trapped during a colony emigration.

With the worker-male connection secured, I made comparisons with material representing 48 contemporary species of *Azteca* and 50 of *Iridomyrmex* (11 Neotropical, 39 Indo-Australian) in the Museum of Comparative Zoology collection, many with workers and males from the same nests. The following characters appear to hold with consistency:

1. In *Azteca* workers the mesonotum is usually moderately convex in side view and hence does not form a smooth line with the pronotum; in New World *Iridomyrmex* workers the mesonotum is only weakly convex in side view and forms a continuous line with the pronotum.
2. In *Azteca* workers the dorsal face of the propodeum is much less convex in side view than in *Iridomyrmex* workers.
3. In *Azteca* workers the petiolar node is longer than high (the reverse is true in *Iridomyrmex*) and inclined more strongly forward than in *Iridomyrmex*.
4. The occiput of *Azteca* workers is usually more deeply concave than in *Iridomyrmex* workers, although extreme species within the two genera overlap.
5. In *Azteca* males, the scape is very short, no longer than the combined second and third antennal segments, while either the second or third segment (depending on the species) is notably elongated, inflated, or both. In *Iridomyrmex* males, the antennae are more typical, with relatively long scapes and unmodified funiculi; an exception is *I. iniquus,* which has the *Azteca* antennal form.
6. In *Azteca* males the mandibles are short and triangular, lacking a well-defined masticatory border; whereas in *Iridomyrmex* males the mandibles have a well-defined masticatory border which also often bears serially arranged teeth.

7. In *Azteca* males the dorsal lobe (digitus) of the volsella is long and finger-like, extending posteriorly as far as the tips of the parameres (see Fig. 6E). They are proportionately broader in *Iridomyrmex* and reach only partway along the length of the parameres.

8. In most cases, the petiole of *Azteca* males is applied more broadly to the gaster than is the case in *Iridomyrmex*.

Using the combination of traits above, it has been possible to establish beyond much doubt that the species of the Dominican amber divide cleanly into either *Azteca* or *Iridomyrmex*, that none falls between the two genera, and that none is especially primitive in overall aspect. The most abundant ant species in the amber is the *Azteca* to be described below.

Azteca alpha, new species
(Figs. 5–8)

Diagnosis. A member of the *alfari* group, in which the worker caste is monomorphic or at most weakly polymorphic; *alpha* is also distinguished from the contemporary species belonging to this and other *Azteca* groups by the unique combination of traits in scape length, propodeal outline, and pilosity illustrated in Fig. 5. In particular, the worker appears especially close to *A. fiebrigi*. This Paraguayan species is distinguished from *alpha* by its slightly shorter scapes (which just reach the occipital corners in repose) and longer, denser body pilosity.

The male of *alpha* (Fig. 6) is close to or identical with that of *fiebrigi*, including the distinctive conformation of the scape and first two funicular segments. Both forms differ from *alfari*, the other member of the species group for which I have seen males associated with workers, in that *alfari* has the scape and first funicular segment short and slender and the second (rather than first) funicular segment conspicuously enlarged.

The queen of *alpha* (Fig. 7), encountered singly in two amber pieces and hence only tentatively associated with the *alpha* worker caste (as opposed to that of *eumeces*, to be described subsequently), is closely similar to the *fiebrigi* queen. It differs in its somewhat thinner petiolar node viewed from the side.

The name *alpha* alludes both to the early occurrence of the species in the geological record and to its numerical dominance in the Dominican amber.

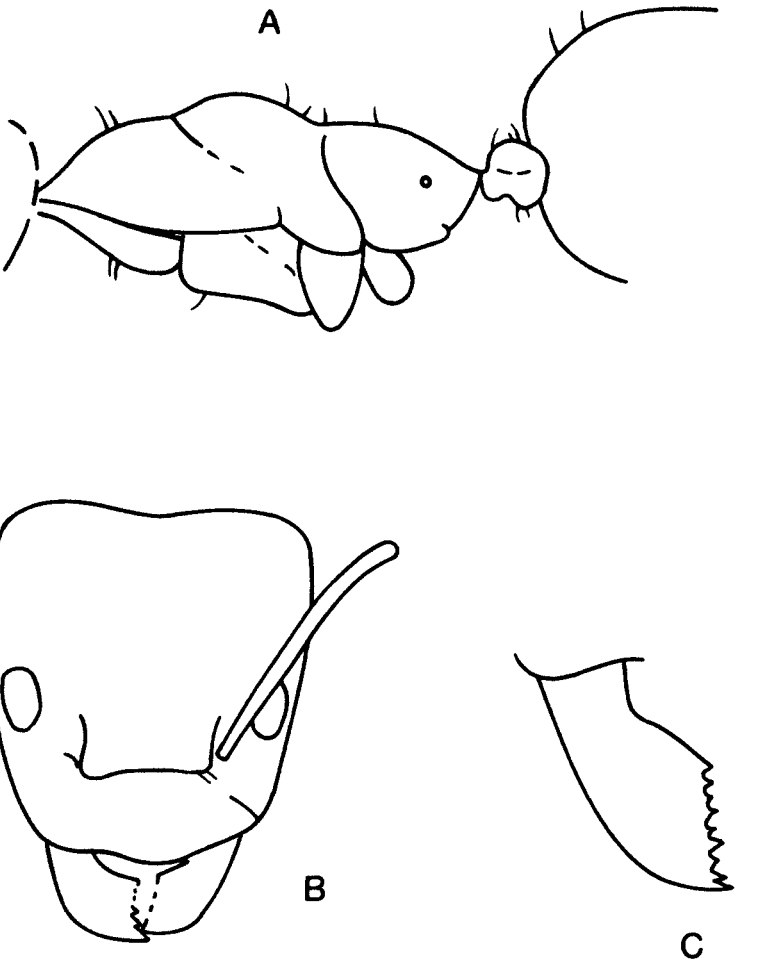

Fig. 5. *Azteca alpha*. A, holotype worker, side view of body; B, head of a paratype worker; C, left mandible of another paratype worker.

Holotype worker. Head Width 0.53 mm, Head Length 0.60 mm, Scape Length 0.48 mm. From a piece of amber with closely intermingled workers and males, known to originate from the Dominican Republic but with no further locality.

Paratype workers. A total of approximately 540 workers in 171 pieces of amber have been placed in *A. alpha*. Most were from

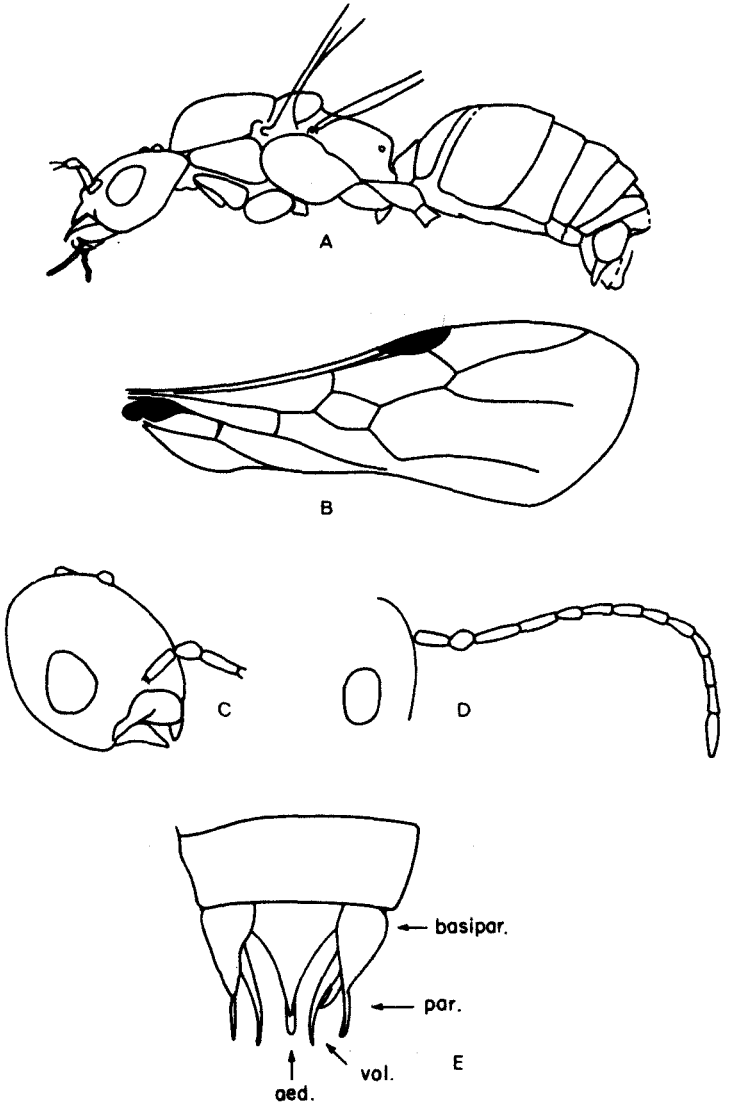

Fig. 6. *Azteca alpha* paratype males associated in same amber piece with holotype worker. A, side view of body; B, left fore wing; C, oblique lateral view of right side of head; D, left antenna; E, dorsal view of genitalia (showing basiparamere, paramere, volsella, aedeagus).

unknown mines in the Dominican Republic, but a large minority originated from the following localities, including almost all from which I have seen ants of any kind: Carlos Diaz, near Tamboril; Cotui; La Bucara; La Cumbre; La Toca; Las Bocas del Licey; Llaroa (Yaroa); Los Cacaos; Marias; Palo Quemado; Bayaguana. The specimens share the key characters of the holotype nest series. They are quite variable in size (Head Width 0.42–1.06 mm overall), but, as documented in Fig. 8, relatively little variation occurs within single amber pieces. Moreover, the size variation in one especially populous piece I have examined appears to be unimodal with little or no skewing. Hence *A. azteca* must be regarded, at least tentatively, as a monomorphic species.

Paratype males. A total of 17 individuals in 8 pieces (3 with associated workers). The essential characteristics, placing the species still more firmly within the *alfari* group and in particular close to *fiebrigi*, are illustrated in Fig. 6. The alitrunk length of the male depicted, from the holotype nest series, is 1.04 mm. The Head Width (including eyes) of another male measured from Palo Quemado is 0.72 mm.

Paratype queens. The elongate head shape of 2 alate queens found in separate amber pieces (Dominican Republic, no further locality) might seem to associate them logically with *A. eumeces*, the second, rarer *Azteca* species occurring in the Dominican amber. Nevertheless, at least some of the contemporary *alfari* group species, in particular *coeruleipennis*, *fasciata*, and *fiebrigi*, have workers with ordinary head shapes and queens with elongated heads. Moreover, the Dominican amber queens closely resemble those of *fiebrigi*.

General remarks. *Azteca alpha* is by far the most abundant ant species and hence probably the most abundant insect species in the Dominican amber. It occurs in 29% (171 of 592) of the ant-bearing amber pieces I have studied closely to date. Since I passed a large percentage of the pieces back to dealers prior to the revisionary work because they contained *A. alpha* and thus were considered of less interest, the actual representation of the species was much higher, very likely 50% or more.

In addition, *A. alpha* workers have been found in the same pieces as many of the other Dominican amber genera: *Pseudomyrmex*, *Crematogaster* (*Orthocrema*), *Oligomyrmex*, *Pheidole*, *Monacis*, *Hypoclinea*, and *Camponotus*. This circumstance, plus the occur-

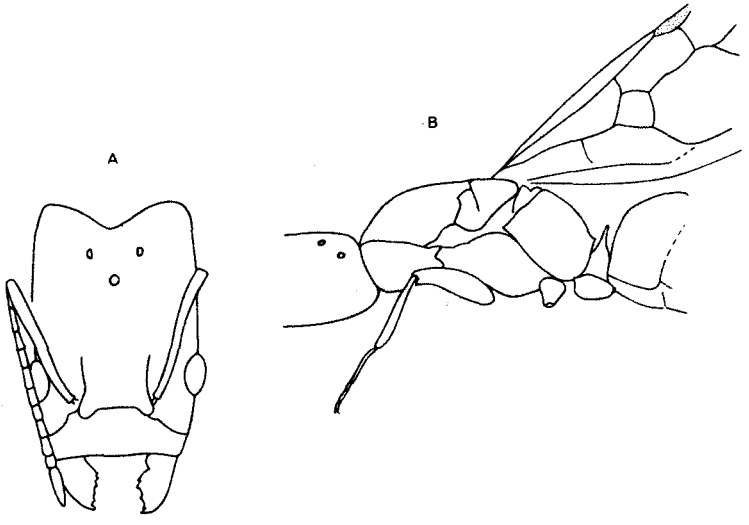

Fig. 7. *Azteca alpha* queen (tentative association). A, head; B, side view of body.

rence of *A. alpha* in pieces from almost all of the identified mines to date (the only exceptions are El Valle and Palo Alto) is evidence that at least the bulk of the Dominican ant fauna is relatively cohesive and did not stretch over a very long period of geological time.

The frequent occurrence of large numbers of *A. azteca* workers in the same amber piece, in a few cases 50 or more, also suggests that the species foraged in groups or at least recruited groups to food sources or enemies. Such behavior characterizes contemporaneous species of *Azteca*. So far as known all of the living *Azteca* species are arboreal, foraging onto the ground only secondarily, and it is reasonable to suppose this was true of *A. alpha* as well. In addition, at least some of the modern members of the *alfari* group are specialized for life on the moraceous tree *Cecropia* (Wheeler, 1942). What this means for *A. alfari*, whose workers were trapped in the gum of the leguminous tree *Hymenaea courbaril* (locust tree or "algarrobo") is unclear.

I have not excluded the possibility that more than one species exists in the large quantity of material placed with *A. alpha*. Many

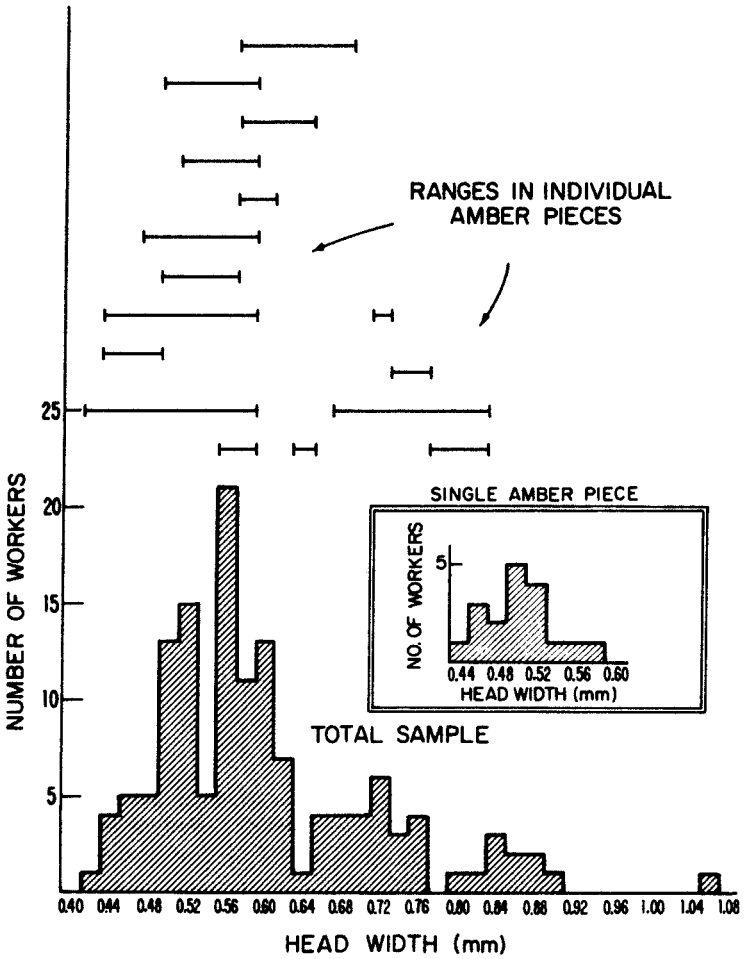

Fig. 8. *Azteca alpha* workers: size range between and within series found within individual amber pieces and hence assumed to belong to the same colony. The larger frequency curve (*bottom in figure*) includes all of the 141 workers measured. The smaller frequency curve (*enclosed in rectangle*) includes the measurable workers from one of the most populous pieces. The series of horizontal bars (*uppermost in figure*) depict the ranges within single amber pieces. The samples originate variously from Carlos Diaz, La Bucara, Las Bocas del Licey, Llaroa, Los Cacaos, Palo Quemado, and still other, unknown mine sites within the Dominican Republic.

of the specimens were so decayed or poorly positioned that the critical characters could not be examined, and in these cases I relied on size and habitus.

Azteca eumeces, new species
(Fig. 9)

Diagnosis (worker). A medium-sized member of the *alfari* group distinguished from all known contemporary members of the genus, as well as the Dominican amber *A. alpha,* by the exceptionally elongate head of the worker (Cephalic Index about 70–80 as opposed to 80 or more in other species). In overall appearance *A. eumeces* is similar to *bicolor, fasciata,* and *theresiae,* but in addition to possessing somewhat less elongate heads, these living species also have more convex lateral sides of the head seen in full-face view, with the outer margins of the eyes located well inside the head margins.

The name *eumeces* is derived from Gr. *eumekes,* of good length.

Holotype worker. Head Width 0.43 mm, Head Length (from line of posteriormost reach of occipital corners to line of center of anterior clypeal border) 0.63 mm, Cephalic Index 68, Scape Length 0.47 mm, Pronotal Width 0.27 mm. In an amber piece from Palo Quemado, near Santiago, Dominican Republic.

Paratype workers. Thirty-eight workers in 6 amber pieces, Dominican Republic (no further locality).

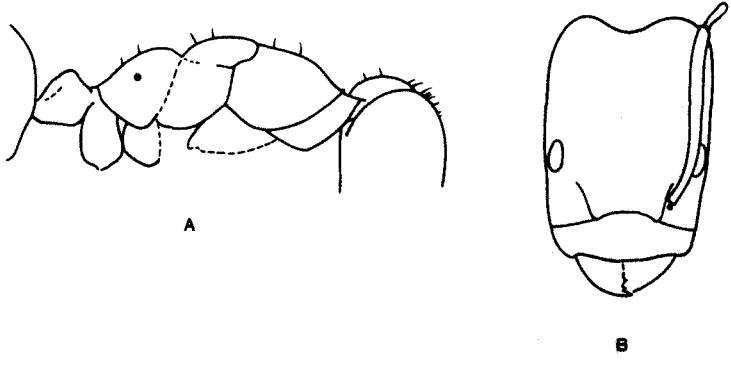

Fig. 9. *Azteca eumeces* holotype worker: A, side view of body; B, head.

Iridomyrmex hispaniolae, new species
(Fig. 10)

Diagnosis (worker). A medium-sized (Head Width 0.5–0.8 mm), slender species similar to the living species *I. pilifer* of northern South America, especially close in details of the head and alitrunk, differing from *pilifer* in its distinctly thicker, less symmetric petiolar scale in lateral view.

Holotype worker. Head Width 0.70 mm, Head Length 0.72 mm, Scape Length 1.03 mm, length of alitrunk 1.08 mm. Body overall smooth to lightly shagreened, and feebly shining. Pilosity very sparse, mostly limited to a few hairs on the head, gaster, and appendages. Body light to medium yellowish brown. Las Bocas del Licey, Dominican Republic.

Paratype workers. Forty-six workers in 32 amber pieces variously from Carlos Diaz, El Valle, La Toca, Llaroa, Los Cacaos, Palo Quemado, and Bayaguana; 19 of the pieces have no further localities other than the Dominican Republic. Head Width 0.52–0.83 mm. All closely similar in habitus to the holotype.

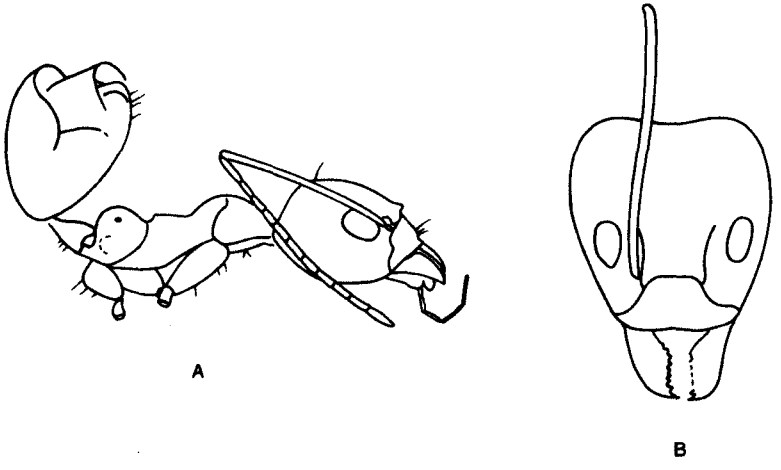

Fig. 10. *Iridomyrmex hispaniolae* holotype worker: A, side view of body; B, head.

I. hispaniolae was also compared with series belonging to 39 Old World *Iridomyrmex* species, including all of the principal species groups. It bears an overall resemblance to certain of them, especially *anceps, emeryi,* and *pallidus,* but differs substantially in various combinations of details in the petiole shape, pilosity, eye size, and sculpturing.

Iridomyrmex humiloides, new species
(Fig. 11)

Diagnosis (*worker*). A relatively small species resembling *I. humilis* of South America. With this living form it differs from other members of the species, including *despertitus* and *pruinosus,* most conspicuously in the concave anterior border of its clypeus. It differs from *humilis* (and other contemporary similar species) by the fact that its eyes exceed the lateral borders of the head in full-face view, whereas in the living species the outer margins of the eyes do not reach the lateral borders of the head.

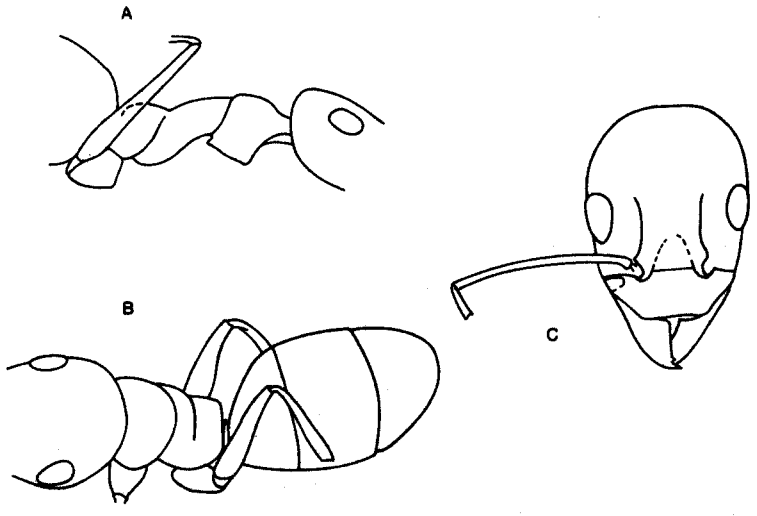

Fig. 11. *Iridomyrmex humiloides* holotype worker: A, oblique dorsal view of head and body; B, lateral view of body; C, head.

Holotype worker. Head Width 0.41 mm, Head Length 0.53 mm, Scape Length 0.60 mm, Eye Length 0.13 mm. Body overall lightly shagreened and feebly shining and subopaque. Body almost completely hairless, light to medium reddish brown in color. Dominican Republic amber: no further locality.

Tapinoma

Although *Tapinoma* is cosmopolitan and composed of numerous, anatomically diverse species, it has not previously been recorded from the fossil record. At least three species (*litorale, opacum, rasenum*) are native to the Greater Antilles while a fourth (*melanocephalum*) occurs there and may either be native or introduced by commerce. The following record establishes the relative antiquity of the genus as well as of the *atriceps* group in the West Indies.

Tapinoma trochis, new species
(Fig. 12)

Diagnosis (worker). A member of the *atriceps* group, distinguished by small size and a conspicuous broadening of the fore femora and tibiae. It most closely resembles *canalis* of Panama among living species, which differs from *trochis* by the fact that its scapes reach the occipital corners. Also, the propodeal dorsum of *canalis* is less flattened in side view, and the dorsal and declivitous propodeal faces meet in a rounded but distinct obtuse angle.

The Greek specific name *trochis* means runner and is meant to refer to the powerful-looking fore legs.

Holotype worker. Head Width 0.32 mm, Head Length 0.37 mm, Pronotal Width 0.21 mm, Scape Length 0.26 mm, Eye Length 0.06 mm. Body smooth, feebly shining to subopaque, devoid of standing hairs, medium yellowish brown. Dominican Republic amber: no further locality.

Species Properly Excluded from the Dolichoderinae

Camponotus neotropicus (Baroni Urbani), new combination

Leptomyrmex neotropicus Baroni Urbani, 1980, *Stuttgarter Beitr. Naturkunde,* Ser. B, 62: 1–10, worker, Type locality: amber, Dominican Republic, no further locality.

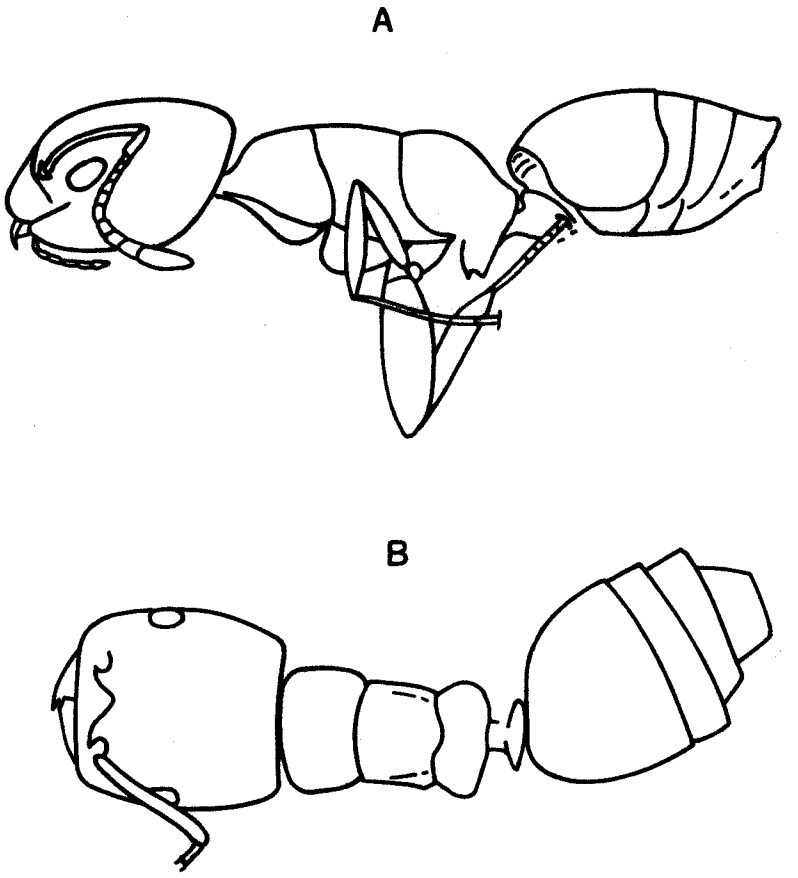

Fig. 12. *Tapinoma trochis* holotype worker: A, lateral view; B, dorsal view.

The living species of *Leptomyrmex* are confined to Australia and Melanesia. All of the other ants thus far discovered in the Dominican amber belong to modern Neotropical genera and, in many cases, living species groups. Hence, as Baroni Urbani (1980) himself noted in his original description, the occurrence of *Leptomyrmex* in the West Indian ant fauna during Dominican amber times would constitute a considerable biogeographic anomaly. The situation is confused by the poor condition and uncertain anatomy of the *Leptomyrmex neotropicus* types, all 8 of which are in the same piece of amber.

During my own study I encountered a single worker in the Museum of Comparative Zoology collection that fits the *L. neotropicus* habitus closely. Although this specimen has the front part of the head missing, there is little distortion in the remainder of the head and body. An apparent acidopore can be seen, placing the species in the Formicinae rather than in the Dolichoderinae. And indeed, the specimen is closely similar to *Camponotus branneri* of Brazil, sharing the same distinctive elongated body form, mesothoracic constriction, petiole, tapered neck, and bulging eyes located toward the rear of the head. *C. branneri* is also similar to *C. santosi* of Cuba and *C. sexguttatus* of Central America and the West Indies.

The status of *neotropicus* will not be settled definitively until additional and better preserved *neotropicus* workers are available. In the meantime, the evidence as well as biogeographic probabilities make it prudent to place the fossil species provisionally in *Camponotus* and to remove the genus *Leptomyrmex* from the Dominican amber faunal list.

Discussion

There has been a remarkable retreat of the Dolichoderinae from the West Indies since Dominican amber times, in other words, since the late Oligocene or early Miocene. Four genera (*Azteca, Dolichoderus, Hypoclinea, Monacis*) have disappeared entirely from the Greater Antilles. Only two (*Iridomyrmex, Tapinoma*) have persisted to the present, while a single genus, *Conomyrma*, has invaded more recently. The dominant arboreal ants are no longer *Azteca*; according to W. L. Brown (personal communication), who has collected intensively over much of the Dominican Republic, the more abundant genera include *Pseudomyrmex, Crematogaster, Paracryptocerus*, and *Camponotus*. In this important respect the West Indian fauna mirrors the general decline of the Dolichoderinae in North and South America, Europe, and Asia, possibly in conjunction with the advance of *Crematogaster* as a competitor of *Iridomyrmex* (Brown, 1973).

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